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Territoriality in a subtropical kyphosid fish associated with macroalgal polygons on reef platforms at Rottnest Island, Western Australia

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Abstract

Kyphosus cornelii, the Western Buffalo Bream, is a relatively large, schooling, herbivorous fish (up to 60 cm total length), endemic to the west coast of Australia, that feeds almost exclusively on rhodophytes. It is shown that individual fish of both sexes defend contiguous, polygonal territories that cover large areas of shallow limestone shoreline platforms. Irregular pentagons and hexagons predominate, delineated by fucoid macroalgal borders that surround areas of predominantly rhodophyte turf. The mean area of each polygon is about 12 m^2. The majority of polygons have five or six sides and have predominantly six adjacent polygons surrounding them. Territorial macroalgal borders commonly disappear seasonally, but subsequently reappear close to their original positions. Three phases of behaviour are recognised in *K. cornelii*: a territorial phase on shoreline platforms, a schooling phase on the platforms, and a schooling phase in deeper water adjacent to the platforms. The territories appear to be associated with feeding and not directly with breeding.

Introduction

Conspicuous polygons formed by brown macroalgae on intertidal shoreline platforms at Rottnest Island Western Australia (32°00'S, 115°30'E), were first recorded by Playford (1976, 1988), but the reason for their distinctive growth form was unknown (Figs 1-3). Playford (unpublished) had also observed and photographed extensive areas of such polygons on the Houtman Abrolhos, 400 km further north, in 1968. Excavation below the macroalgal borders showed that they were not controlled by joints or other features of the limestone substrate. A clue to their possible link with fish territories was provided by an illustration by Robertson (1989) of "hedgerows" of macroalgae separating territories of the surgeonfish *Acanthurus lineatus* at Moorea in the Pacific. This led to the present study which records that the Rottnest polygons are indeed occupied and apparently maintained as fish territories, by the Western Buffalo Bream, *Kyphosus cornelii* (Whitley 1944).

The aim of this paper is to describe the behaviour of *K. cornelii* in relation to the polygons and to discuss how and why polygons may be associated with its territoriality. Studies of the reproductive biology of *K. cornelii* and detailed studies of feeding in relation to polygon formation and composition of the algal turf within the polygons are proceeding.

K. cornelii is endemic to the west coast of Australia between Cape Leeuwin 33°22'S, 115°08'E and Coral Bay 23°07'S, 113°45'E (Hutchins & Thompson 1983). Shoals of up to several hundred individuals are common on shallow limestone shoreline platforms. It is sympatric over most of its range with *Kyphosus sydneyanus* (Günther 1886), the distribution of which extends to south-eastern Australia (Scott 1962, Hutchins & Swainston 1986) and New Zealand (Doak 1972). Both are relatively large herbivores; *K. cornelii* grows up to 60 cm total length and *K. sydneyanus* up to 80 cm total length (Hutchins & Thompson 1983).

Rimmer (1986) and Rimmer and Wiebe (1987) describe unique digestive tracts and fermentative digestion in these two kyphosid species. They also show that adults of both species browse exclusively on benthic macroalgae and that the food resource is partitioned, with *K. cornelii* feeding selectively on Rhodophyta (91.9% of diet) and *K. sydneyanus* feeding selectively on Phaephyta (93.9% of diet).

Shoreline platforms fringe most of Rottnest Island and range from a few metres to about 200 m in width. They are cut almost horizontally into eolianite of the Tamala Limestone. According to Playford (1988), their mean elevation is -0.41 ± 0.11 m Australian Height Datum (AHD, mean sea level) which is about 0.2 m below mean low water level. A platform of this level would be exposed for about 3% of each year (D F Wallace, personal communication).

Hodgkin & DiLollo (1958) described the tides of south-western Australia in detail and commented on their unusual nature. Tides at Rottnest Island differ little from those at the nearby port of Fremantle (D F Wallace personal communication). They are predominantly diurnal, with only one high and one low water in each 24 hours, with low water at about the same time on successive days, but getting gradually earlier throughout the year. Semi-diurnal and mixed tides also occur. However, the daily astronomic tidal range is small, so that atmospheric pressure and wind produce changes of at least the same order of magnitude, making tidal height rather unpredictable. Daily tidal range rarely exceeds 1 m and is generally much lower. Mean annual sea level is about 30 cm higher in winter than in summer. It also varies from year to year over a range of about 15 cm, and Pearce & Phillips (1988) have shown that a high correlation exists between years of low mean sea level at Fremantle and El Nino/Southern Oscillation (ENSO) years, and this is thought to be associated with reduced flow of the Leeuwin Current.

Material and Methods

This work, unless otherwise stated, was undertaken at Wilson Bay on the south side of Rottnest Island. Algal polygons have been photographed (by PEP) at Rottnest Island intermittently since 1976. Photographs from Playford (1988) are reproduced here (Figs 1 and 2) because this

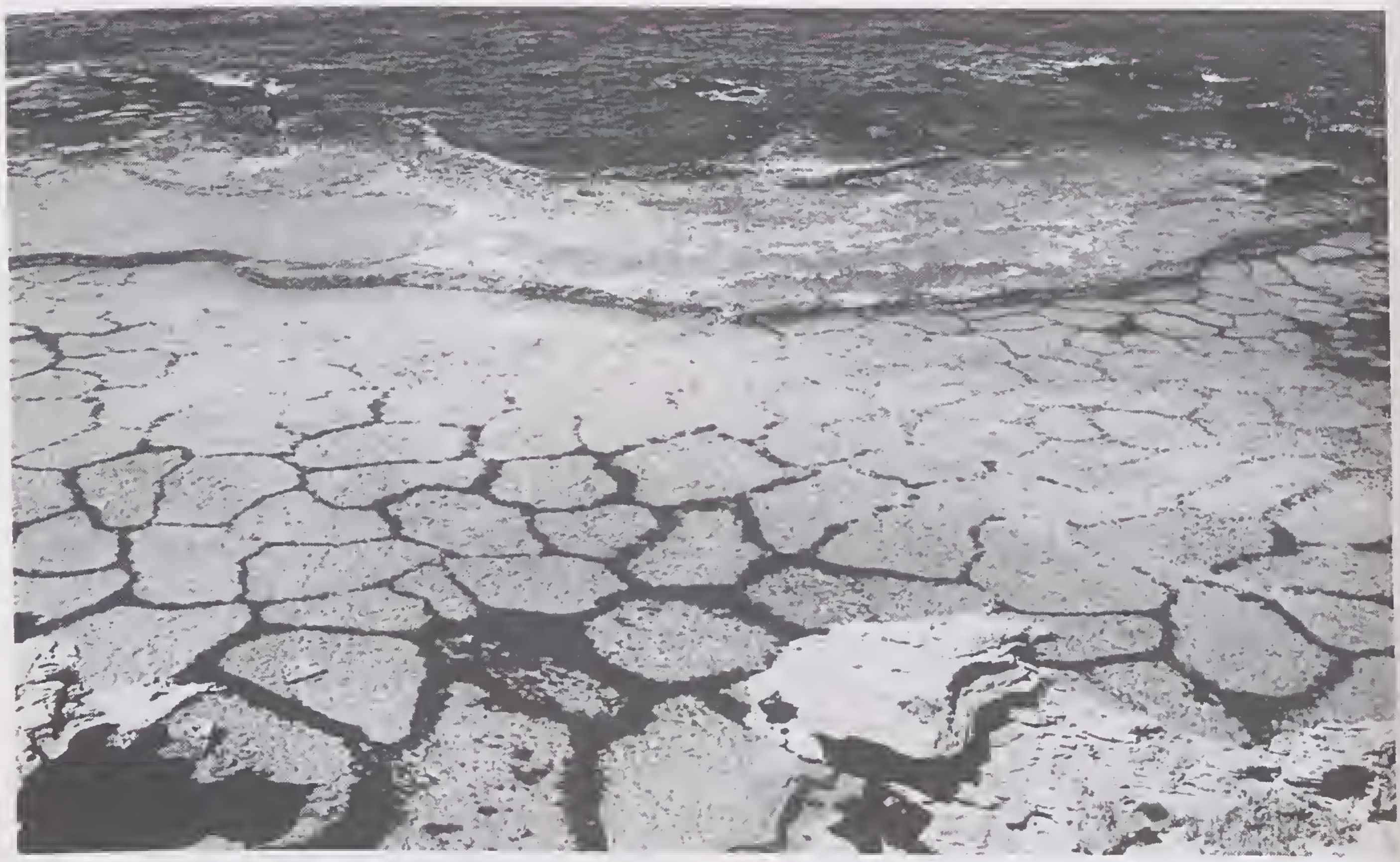

Figure 1. Wilson Bay, October 1985, showing well developed algal polygon formation covering the entire shoreline platform. Reproduced from Playford (1988).

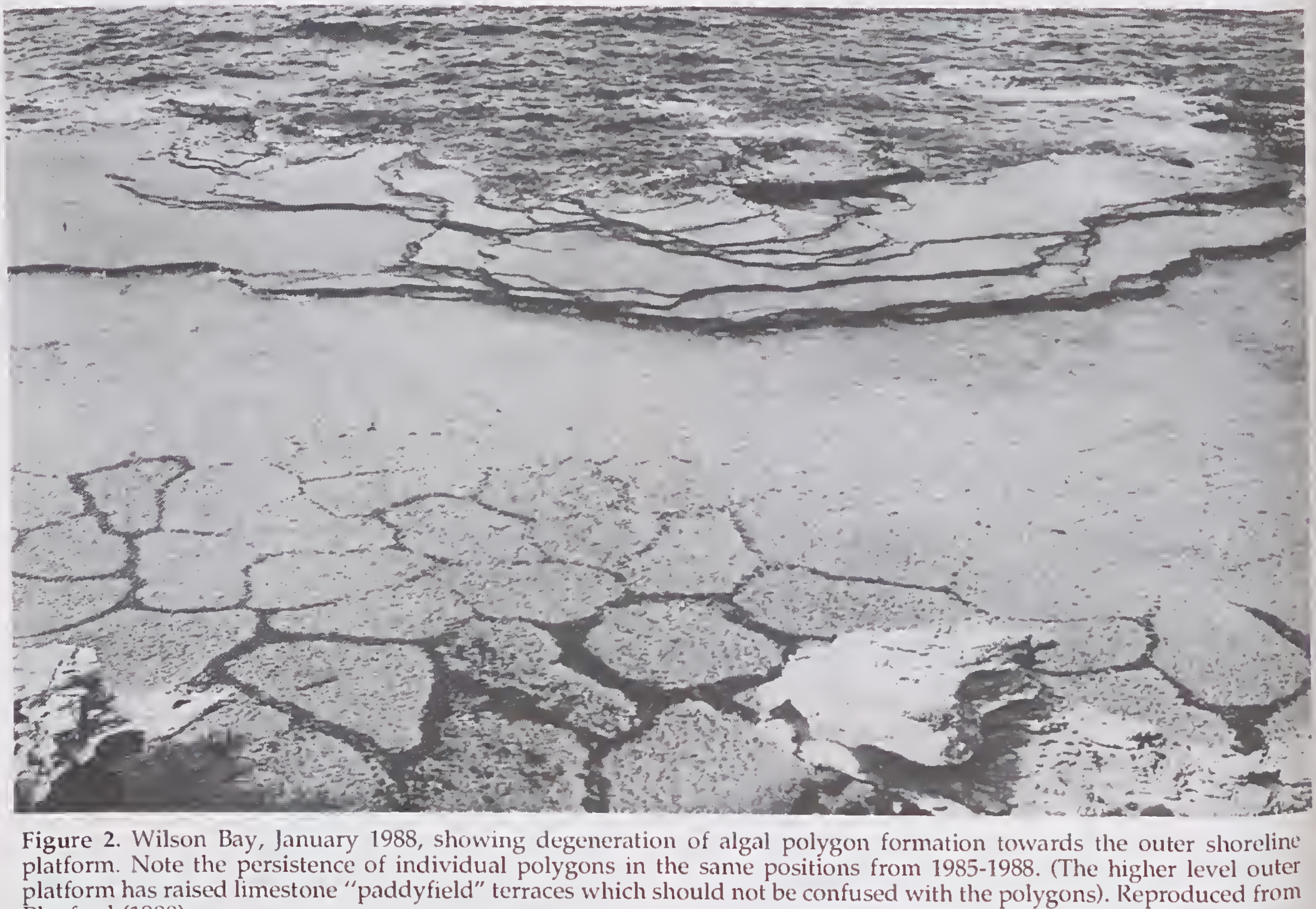

Figure 2. Wilson Bay, January 1988, showing degeneration of algal polygon formation towards the outer shoreline platform. Note the persistence of individual polygons in the same positions from 1985-1988. (The higher level outer platform has raised limestone "paddyfield" terraces which should not be confused with the polygons). Reproduced from Playford (1988).

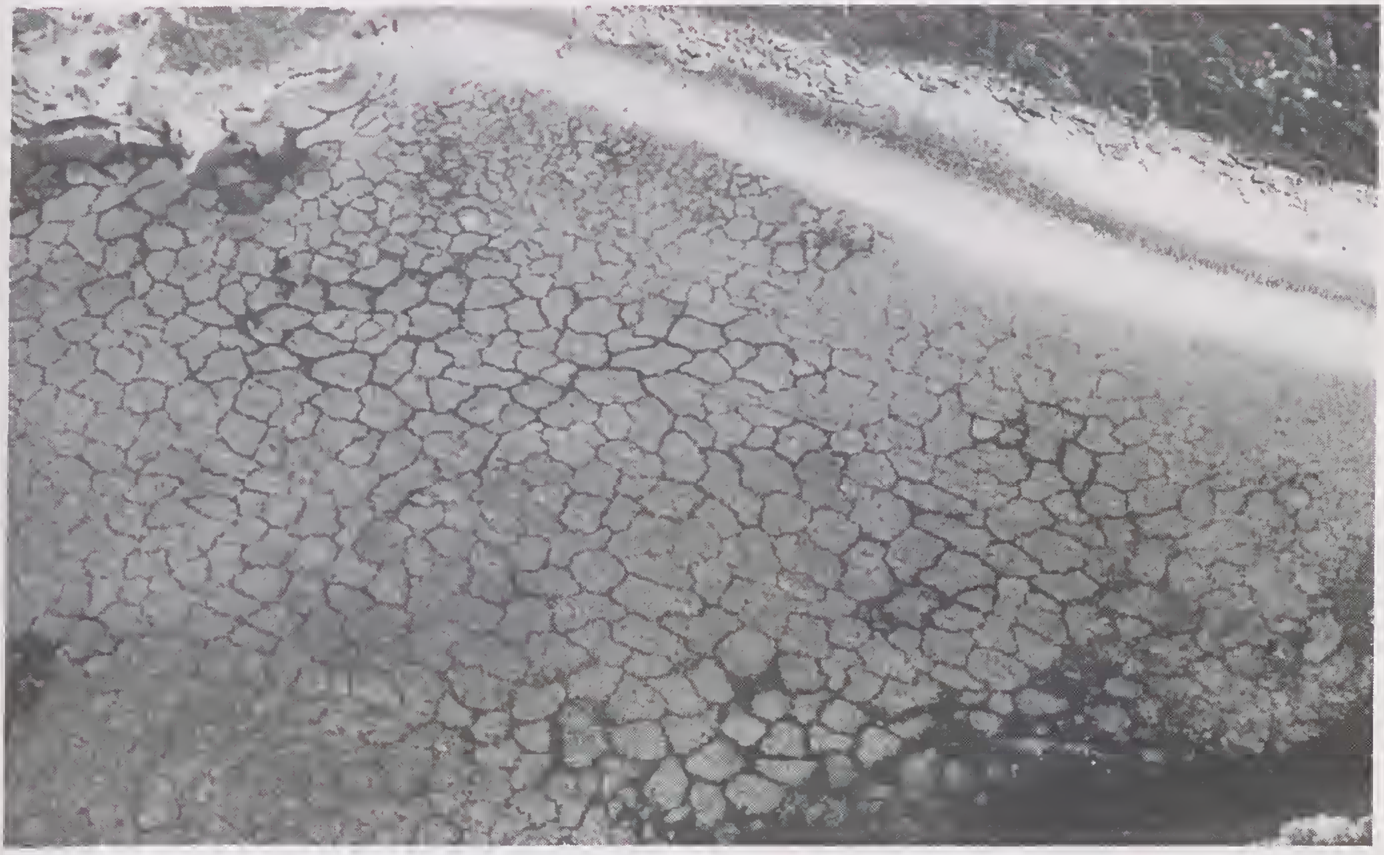

Figure 3. Aerial view of algal polygons on Radar Reef shoreline platform, Rottnest Island, in November 1991, showing a group of smaller polygons adjacent to the shore.

reference is not readily available outside Western Australia.

The average area of the polygons was estimated from enlargements (x 4) of 1:15,840 aerial photographs (Series WA 1420C, Rottnest Island, 16 October 1972). The number of sides of polygons and the number of adjacent polygons were determined from aerial photographs and photographs taken from cliffs above the shoreline platforms. In determining the number of sides in a particular polygon, the criterion for counting a side, whether straight or curved, was whether it was separated from the next side by a corner, and not by the number of polygons in contact with that side. Thus it was possible for a side to have more than one territory in contact with it. The same criterion was used by Clayton & Vaughan (1982) in their study of mudskipper territories.

Observations and underwater photography of fish were done (by PFB) by snorkelling on 15 separate dates between March 1990 and July 1991 inclusive. The only months not covered during this period were September, December and February. A supplementary sample of eight territorial fish was added in February 1992.

Frequency of browsing and aggressive interactions was scored for individual fish that were each watched for a minimum period of five minutes. These observations were undertaken at the same time of day, thus avoiding possible daily cycles in feeding activity affecting feeding rate scores of territorial and schooling fish.

A total of 33 fish were speared for examination of gonads and stomach contents. Of these 11 were territorial, 2 were schoolers (vagrants) from the reef platform and the balance were from deeper water adjacent to the reef platform. The small number of vagrant fish sampled from the platform reflects their timid behaviour in shallow water, making them difficult to shoot. Fork length (FL) was measured from the tip of the snout to the middle of the tailfork. Gonads of 24 fish were fixed in 10% formaldehyde for histological examination. Stomach contents of 11 fish were preserved in formaldehyde and examined microscopically and stomach contents of 19 others fish were examined fresh, using a hand lens, to confirm Rimmer & Wiebe's (1987) finding that this species feeds almost exclusively on Rhodophyta.

Results

Description of polygons

Contiguous algal polygons, formed by narrow borders of fucoids (predominantly *Sargassum*) surrounding areas of short (predominantly rhodophyte) turf, covered extensive areas of intertidal and shallow subtidal shoreline platforms in the study area, extending to maximum water depths of about 1.5 m (Figs 1-3). Irregular pentagons and hexagons predominated (Fig 4A). However, the majority of polygons had six adjacent polygons surrounding them (Fig 4B). The mean maximum length was 6.1 m ± 0.89; maximum width (perpendicular to the maximum length) was 3.6 m ± 0.74; and mean area was about 12 m^2, within a range of about 5 to 20 m^2. The shared fucoid borders were approximately 10 to 35 cm wide and ranged in height from a few centimetres to approximately 20 cm.

Aerial photographs showed that the polygons within groups tended to be of relatively constant size, but with large size variations from one group to another, sometimes on the same platform (see Fig 3). The approximate average area of individual polygons in the main group at Wilson

Bay (aerial photograph Number 5003, series WA 1420) was 13 m^2 (ranging from about 10 to 18 m^2), whereas in a large group at the eastern end of Strickland Bay (aerial photograph Number 5004) the approximate average was only 7 m^2 (ranging from about 5 to 9 m^2). Elsewhere some groups attained average polygon areas of as much as 16 m^2.

The degree of development of the fucoid polygon borders varied seasonally, and most polygons gradually degenerated and disappeared (Figs 1 and 2), leaving some areas of the reef platform entirely dominated by turf, only to reappear close to their original positions. This is attributed to regeneration of *Sargassum* thalli from perennial holdfasts.

In 1990-91 both the degree of polygon development and the total area covered by polygons all around Rottnest Island were observed to increase in spring (September-November) and thereafter to decline. This corresponds with rapid growth of *Sargassum* thalli in spring, culminating in release of gametes in November, followed by senescence and loss of thalli thereafter (G Kendrick, personal communication).

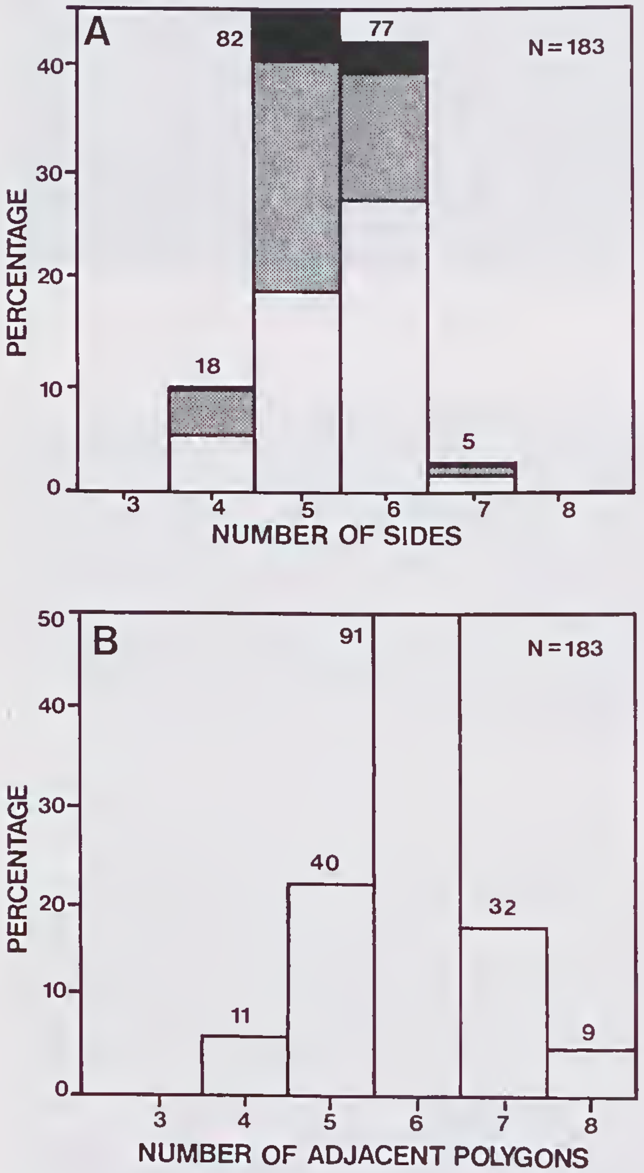

Figure 4. A Frequency distribution of number of sides of algal polygons at Wilson Bay. Shown within each column is the proportion of territories having the same number of adjacent polygons as the number of sides (blank), one more (stippled) and two more (black). B Frequency distribution of number of surrounding, adjacent polygons (neighbours).

At Wilson Bay the fucoid borders of the polygons in deeper water, towards the outer edges of shoreline platforms, showed more pronounced seasonal decline and were more prone to total disappearance than those towards the shore, which persisted throughout the 1990-91 study period. A comparison of a photograph taken at Wilson Bay in 1976 (Playford 1976) and again in 1988 (Fig 2) demonstrates that the polygons have persisted at Wilson Bay since 1976 in similar positions to those illustrated in 1988. They were still in similar positions during this study.

Polygons were observed to form within extensive (continuous) stands of *Sargassum* between September and November 1990 on shoreline platforms at various localities around Rottnest. By March 1991 most of these polygons had disappeared and some platform surfaces were entirely covered by rhodophyte turf. Aerial photographs taken in March 1990 (Series WA 2851C, 11 March 1990, 1:15,000) similarly showed very few polygons in areas where they were formerly extensive.

Territoriality in Kyphosus cornelii

Three phases of behaviour are recognised in *K. cornelii*: a territorial phase on shoreline platforms, a schooling phase on the platforms, and a schooling phase in deep water adjoining the platforms.

1. Platform territorial phase

Whenever the water level over the shoreline platform at Wilson Bay was greater than approximately 40 cm, each polygon was observed to contain a single, large (> 25 cm fork length) specimen of *K. cornelii* (see Fig 5). Each fish moved about continuously within its polygon, browsing on algal turf, but also interacting aggressively with neighbouring fish along the common macroalgal borders between polygons. The fish faced each other briefly and then swam, sometimes rapidly, for a short distance opposite each other on either side of the border, usually stopping at the nearest corner to face each other again. Territory-holders also showed aggression towards vagrant schools of grazing *K. cornelii* that entered their territories, tending to concentrate on one or two individuals which they sometimes pursued for some distance outside their territories, before returning (see Table 1 for frequency of browsing and aggressive interaction). The shoreline platforms were generally devoid of any other herbivorous fishes, except occasional schools of *Girella zebra* and small (< 15 cm FL) *K. sydneyanus*. The territory-holding fish showed aggression towards *G. zebra* and *K. sydneyanus*, and also *Rhabdosargus sarba*, a bottom-feeding carnivore, but ignored the pelagic, carnivorous Australian Herring, *Arripis georgianus*.

Territory holders were relatively tame, provided that the water depth over the platform was high and the algal borders of polygons were well developed; a fish would generally remain in its polygon despite the presence of a diver, although it became more active. As the water level fell with the tide the fish would become progressively less approachable, and territory holding itself became less pronounced, with fish spending less time in territories and tending to join vagrant schools. Once the water level dropped to approximately 40 cm, very few fish remained territorial. In winter, when polygon borders were poorly developed, territorial fish were extremely nervous and would not remain when a diver entered their polygons, even if water depth was high.

Table 1

Comparison of frequency of browsing and aggressive interactions between non-territorial vagrants and territorial fish on shoreline platforms. N is the number of fish observed in each category, SD is standard deviation, t is students t-value, df is degrees of freedom and P is the probability that the means are the same.

	Browsing (Bites/min)		Aggressive Interaction (Encounters/min)	
	non-territorial	territorial	non-territorial	territorial
Mean	1.70	1.68	0.32	1.66
SD	1.64	1.66	0.33	1.03
Range	0-5.2	0-6.4	0-0.6	0-6.4
N	23	19	13	19
t	0.03		– 4.40	
df	40		30	
P	0.979		<0.001	

Territory holders that were shot were replaced by other fish within the hour in most cases, but this requires further study. Preliminary observations also indicate that individuals hold the same territories for prolonged periods, in the order of weeks or even months.

Eleven territory holders were shot, of which six were females (FL 38.8, 36.8, 31.3, 26.4, 41.8 and 31.7 cm) and five were males (FL 36.5, 35.7, 35.8, 34.7 and 40.1 cm). All had full stomachs containing mainly fleshy red algal turf species. The presence of *Sargassum* fragments and plantlets in the stomachs of all territorial fish sampled provides preliminary evidence that brown macroalgae are browsed from within territories, thus maintaining dominance of turf species within the fucoid borders.

The gonads of all territory holders sampled indicated that spawning was imminent or had recently occurred.

2. Platform schooling phase

At the same time that individuals were defending territories, schools of up to several hundred *K. cornelii* moved about continuously, browsing over the entire shoreline platform, including the territorially held polygons. The fish in these schools or aggregations are termed 'vagrants', as individuals within them moved about apparently at random and rather independently of one another. Occasional aggressive interaction between vagrants occurred (see Table 1), but this was not related to a fixed territory. Despite the aggression of polygon territory holders, schools of vagrants were able to feed within territories for brief periods (a few seconds during which some fish were able to take a bite of turf), because the territory-holding fish directed its aggression towards one, usually large, vagrant individual and because vagrants were constantly on the move between territories (see Table 1 for frequency of browsing and aggressive interaction). Schools included both small fish (down to approximately 15 cm FL) and large fish, whereas territorial fish were exclusively large (> 25 cm FL).

Vagrant fish were less approachable than territory-holders, and their timidity increased as water depth over the platform decreased. Once the water depth dropped below approximately 40 cm the schools tended to move over the outer platform edge to adjacent infratidal waters. However, schools continued to feed intermittently on the

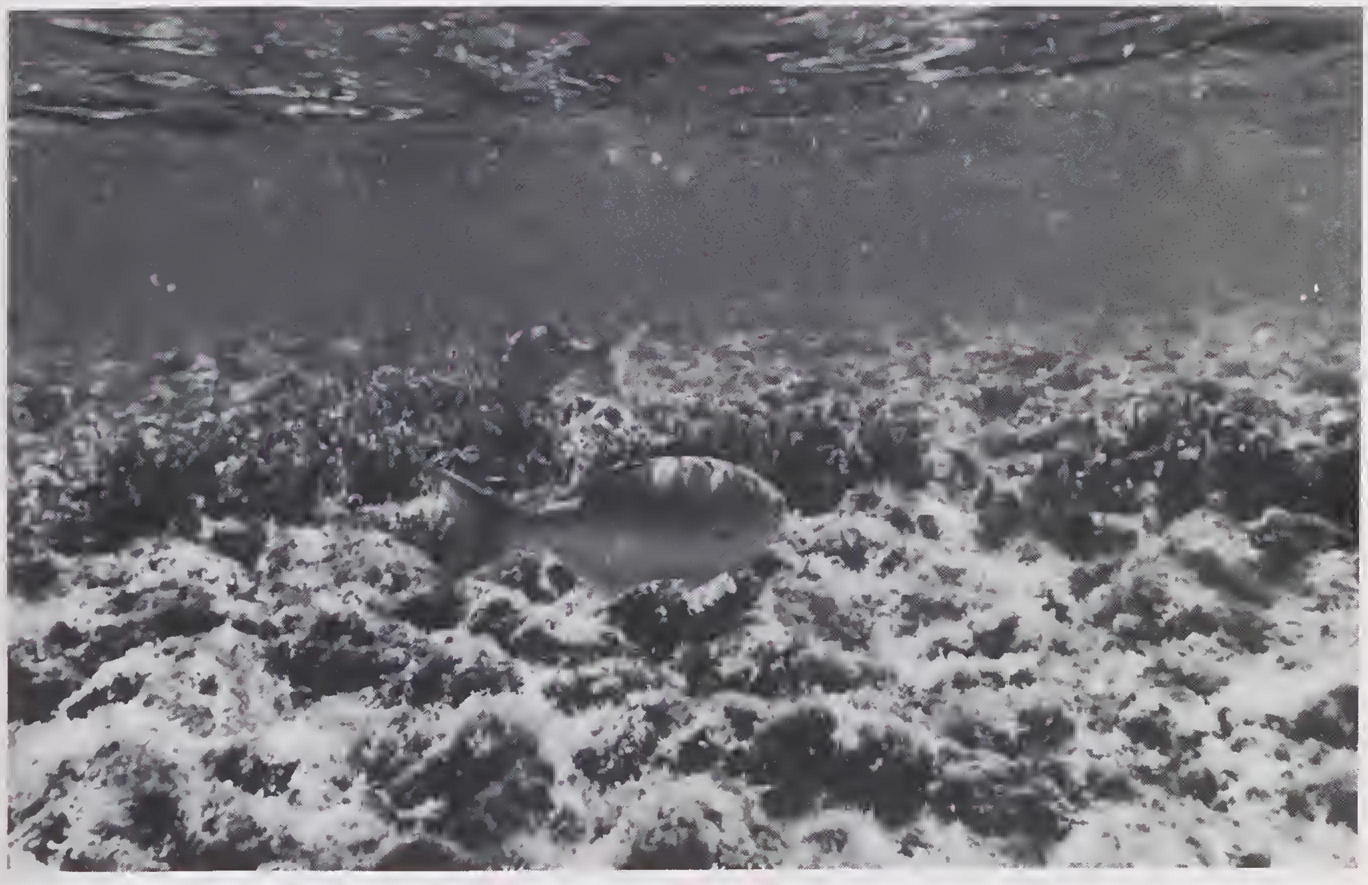

Figure 5. Photograph showing two territorial *Kyphosus cornelii* separated by a fucoid "hedgerow" on the shoreline platform at Wilson Bay, Rottnest Island.

shoreline platform with water depths as low as 30 cm, tending to move on and off with wave surges. Two vagrant fish were shot (FL 47.0 and 32.7 cm). Both were large females and their stomachs were full of predominantly fleshy red algal turf species. The gonads of both were in a ripe, pre-spawning state.

3. Off-platform, deepwater schooling phase

As the water depth over the shoreline platform dropped below approximately 30 cm, all *K. cornelii* moved infratidally and congregated in large schools in the adjacent undercut caves and crevices. These schools, which often intermingled with the infratidal *K. sydneyanus*, appeared to remain within a limited range. Their movements appeared random and aimless; little browsing was observed and individuals occasionally picked pieces of drifting algae from the water column. When disturbed, the fish took shelter in deep crevices. As the water depth over the shoreline platforms increased, fish started to make feeding forays onto the platforms and entered the platform schooling and territorial phases again. Fish in the deep water off the shoreline platforms were relatively tame and easier to sample. Eighteen were shot (FL 27.5-47.4 cm), comprising 8 males and 10 females. All stomachs contained predominantly fleshy red algal turf species.

The cycle of activity described above appeared to be entirely dependent on tidal depth on the reef platforms. Fish were observed to be present on the platform on all three occasions that night dives were undertaken. On one moonlit night they were observed feeding. However, it has not been established whether natural illumination is adequate or necessary for *K. cornelii* to feed on all nights. This cycle of activity contrasts with distinct, regular daily cycles of feeding activity common in herbivorous fishes, for example, marked peaks of feeding in the afternoon (Polunin & Klumpp 1989).

Ripe or spent gonads were recorded in February, March, April, July, October and November, indicating that *K. cornelii* probably breeds throughout the year, although larger samples are required to verify this.

Discussion

Answers as to why and how algal polygons develop on Rottnest Island shoreline platforms are likely to be found in the rather unusual conditions prevailing on them, particularly: the unpredictable and frequently very shallow depth of covering water; the extremely high density and biomass of *K. cornelii* and its relatively large size and high mobility; and the almost exclusive reliance of *K. cornelii* on red-algal turf species for food.

These factors would be expected to result in competition for the food resource and hence the likelihood of behaviour that maximises availability and productivity of palatable red-algal turf species and minimises unpalatable species, including the brown macroalgae that form the polygon borders.

The social behaviour of *K. cornelii* appears to be similar in some respects to that of the parrotfish *Scarus croicensis* from Panama, in which some individuals hold permanent territories while others form feeding schools (Robertson *et al.* 1976). The authors propose that schooling in *S. croicensis* is a mechanism for circumventing territoriality of a competitive, omnivorous damselfish and also territorial conspecifics, as individual schooling fish are attacked less often than non-schooling non-territorials. Given the existence of territoriality in *K. cornelii*, schooling may also allow a higher level of browsing intensity to be achieved.

Reasons for territoriality and algal-polygon formation in relation to *K. cornelii* are not clear. There is no evidence at this stage, in the form of observations of spawning, that territoriality is directly related to breeding behaviour; also, both sexes were recorded as territory holders. Table 1 shows that there is no significant difference in the rate of browsing between territorial and non-territorial fish. However, each territorial fish benefits from almost exclusive access to a considerable area (5-20 m^2/fish, based on the polygon areas), although it engages in significantly more aggressive interactions to achieve this than non-territorial fish. The density of non-territorials (comprising both large and small fish) could not be accurately determined, but it was estimated to be not more than 3 m^2/fish, and individuals covered considerable distances in the course of feeding. It is therefore suggested that territoriality may be a mechanism to ensure adequate nutrition for at least a portion of the breeding component of the population.

The reason for the relative constancy in size of algal polygons within individual groups and the variation from one group to another is not known. It could be a function of local rhodophyte productivity, size of fish, water depth, or some other factor. Further work is needed to solve this important question.

In the shallow water covering the shoreline platforms *K. cornelii* is very vulnerable to attack by Ospreys (*Pandion haliaetus*) which have been observed to prey on it. It seems that the macroalgal borders of the polygons may provide some protection from predation on the otherwise bare platforms, as perhaps indicated by the difference observed in tameness of fish in relation to both water depth and

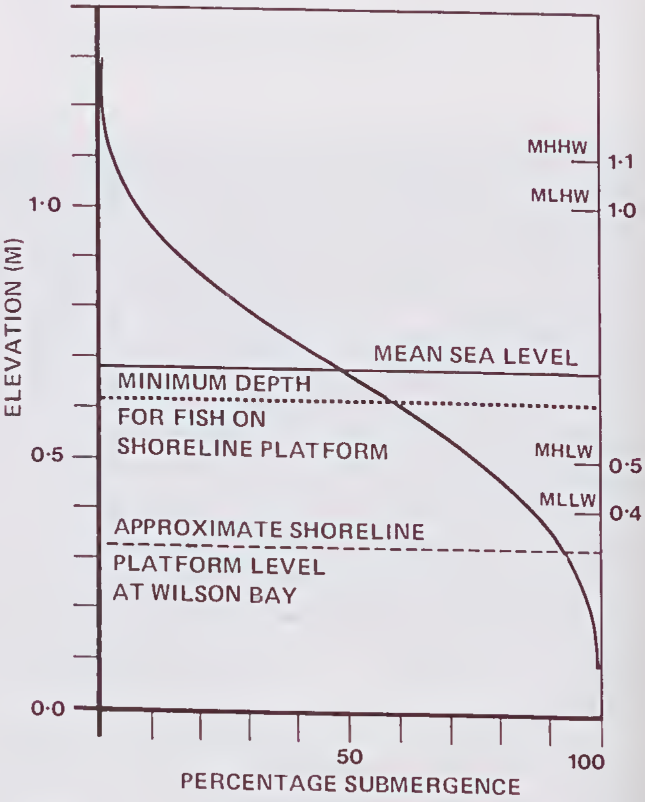

Figure 6. Tidal submergence curve for Rottnest Island showing minimum depth for fish on shoreline platform and approximate shoreline level at Wilson Bay. Elevation refers to height above Tidal Datum (0.0 m). This region experiences a semi-diurnal tidal regime. When two tides occur each day, one is higher than the other. Therefore, the mean higher high water (MHHW), lower high water (MLHW), higher low water (MHLW) and lower low water (MLLW) are indicated separately on the vertical axis.

degree of development of polygon borders. The possible increased danger of Osprey attack when the water depth falls below a critical level (about 40 cm) may also be the reason why the fish desert their territories.

A submergence curve (Fig 6) shows that a relatively small change in mean depth would have a significant effect on the time that *K. cornelii* is able to spend browsing on the Wilson Bay platform. The 30 cm higher average water level over shoreline platforms in winter would be expected to result in a higher level of browsing and territorial activity than in summer.

Formation and maintenance of the macroalgal borders of the territories must involve behavioural interactions between neighbouring territory holders. Robertson (1989) briefly describes "hedgerows", principally of *Turbinaria*, separating neighbouring territories of *Acanthurus lineatus* in Moorea, French Polynesia, which are the closest approximation to *K. cornelii* territories we have found in the literature. He suggests that the hedgerows arise because neighbours do not graze along their common territory borders. Because territorial *K. cornelii* holders browse right up to common territory borders and the demarcation between turf and fucoid borders is so abrupt, it appears that a critical distance may be involved between neighbouring fish below which they do not feed. No displacement feeding activity was observed associated with territorial interactions that could account for the sharp delineation between turf and fucoid borders.

Theoretical reasons for the occurrence of polyhedral and particularly hexagonal shapes in nature have been examined by Thompson (1942). Grant (1968) considered territory shape in terrestrial vertebrates (mainly birds) in structurally simple homogeneous environments and suggested that, theoretically, hexagonal territories will result if territory sizes are similar and neighbours equally spaced. In fishes hexagonal territories have been described for *Tilapia mossambica* (Barlow 1974) and the mudskipper *Boleophthalmus bodarti* (Clayton & Vaughan 1982). At high densities and in a uniform environment the proportion of hexagonal nesting territories in *T. mossambica* increased to 39% at the expense of those with four sides or fewer, but pentagons remained the modal shape with no change in frequency (47%). In *B. bodarti* pentagons also predominated (54%) irrespective of polygon density but there was no increase in frequency of hexagons (30%) at higher densities, which is attributed to differences in territory size. In *K. cornelii* the frequency of hexagons (42.1%) relative to pentagons (44.8%) is higher than in either of these two species. In addition the modal number of adjacent territories is clearly six (Fig 4B) whereas in *B. bodarti* the mode was five despite some polygons having more adjacent territories than sides. Barlow (1974) indicated that social factors, in addition to the geometrical explanation of efficiency of packing, may play a role in determining polygonal territory shapes. In *K. cornelii* the distinct mode of six adjacent territories (largely the result of the high frequency of pentagonal territories with one or two more neighbours than sides) appears to support this suggestion. Simultaneous three-fish confrontational interactions were often observed at the "triple junctions" characteristic of the hexagonal and pentagonal polygon arrangement. It is suggested that there may be behavioural reasons favouring three-way interactions which in turn may determine the angle of corners and number of sides to polygons.

In conclusion, more work is required, not only on the behaviour of *K. cornelii*, but also on the effect this fish has on the dynamics of benthic reef platform communities at Rottnest Island and elsewhere. Algal polygons have recently been observed at several localities on shoreline platforms between Rottnest Island and the Houtman Abrolhos, and further investigation may show that they are more extensive along this coastline than was previously realised.

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